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Possible hominin footprints from the late Miocene (c. 5.7 Ma) of Crete?



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ABSTRACT

We describe late Miocene tetrapod footprints (tracks) from the Trachilos locality in western Crete (Greece), which show hominin-like characteristics. They occur in an emergent horizon within an otherwise marginal marine succession of Messinian age (latest Miocene), dated to approximately 5.7 Ma (million years), just prior to the Messinian Salinity Crisis. The tracks indicate that the trackmaker lacked claws, and was bipedal, plantigrade, pentadactyl and strongly entaxonic. The impression of the large and non-divergent first digit (hallux) has a narrow neck and bulbous asymmetrical distal pad. The lateral digit impressions become progressively smaller so that the digital region as a whole is strongly asymmetrical. A large, rounded ball impression is associated with the hallux. Morphometric analysis shows the footprints to have outlines that are distinct from modern non-hominin primates and resemble those of hominins. The interpretation of these footprints is potentially controversial. The print morphology suggests that the trackmaker was a basal member of the clade Hominini, but as Crete is some distance outside the known geographical range of pre-Pleistocene hominins we must also entertain the possibility that they represent a hitherto unknown late Miocene primate that convergently evolved human-like foot anatomy.

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1. Introduction

Fossil tracks provide information about the presence of a trackmaker at a moment in space and time. Inferring a trackmaker from a trackway is only possible where there is sufficient and distinct morphological data to make the link between trace and culprit. A track is produced by the interplay between the shape/anatomy of the foot and the pattern of loading, mediated through a compliant substrate that is sufficiently elastic to deform yet rigid enough to retain the impression. The variables at play here are

complex and a single trackmaker may produce a range of tracks (e.g., Brand, 1996; Bennett et al., 2014; Milner and Lockley, 2016). In many cases detailed knowledge of a trackmaker's pedal anatomy may be unknown. It is therefore not surprising that ichnologists practice parataxonomy in classifying traces; only where there is sufficient data to infer a trackmaker do they make a more formal link to conventional palaeontological taxonomy. Where such linkages are made they can have controversial implications, especially where body fossils are absent from comparable locations and stratigraphic intervals (e.g., Stössel, 1995; Niedźwiedzki et al., 2010; Voigt and Ganzewski, 2010; Brusatte et al., 2011; Lichtig et al., 2017). Here, we report an example of the challenges of making such inferences when the implications run counter to conventional views on human evolution: hominin-like

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footprints from the late Miocene of Crete, at least 5.6 million years old and thus approximately 2 million years older than the hominin trackways from Laetoli in Tanzania (Leakey and Hay, 1979; Leakey and Harris, 1987; White and Suwa, 1987; Deino, 2011).

2. Material and methods

Two tracked surfaces (A and B2) were found in a natural outcrop above the beach (N 35° 30.857', E 023° 37.660'), close to the village of Trachilos, west of Kissamos (also known as Kastelli), in the Chania Prefecture of Crete (Figs. 1 and 2). The track-bearing surfaces remain in situ in the field and fortuitously are located within a preexisting designated archaeological heritage site. The whole of surface B2 was laser-scanned using a hand-held scanner (ZScanner™ 800 HR with XYZ resolution 50 µm, provided by the company “3DLab”, Warsaw, Poland), producing a detailed 3D

record. Individual prints from surfaces B2 and A were also scanned at higher resolution. Scans were processed in VGStudio Max 2.2 and Adobe Photoshop 12.1. In addition to the scans, the surfaces were photographed in low-angle light to bring out the details of the prints, and surface B2 was cast *in situ* using silicone rubber. The silicone peels were used to produce Jesmonite plaster replicas of the original surfaces. Silicone peels, and polymer clay and plaster casts of individual footprints, have been accessioned to the JuraPark collection (Ostrowiec Świętokrzyski, Poland) under the comprehensive catalogue designation N233. The tracks were also measured in situ with calipers and a tape measure.

Digital morphometric measurements were performed using DigTrace (Budka et al., 2016; www.digtrace.co.uk) and landmarks exported for analysis. Landmarks were placed around the track outlines by multiple observers to form a consensus around placement. Similar landmarks were placed on comparative track

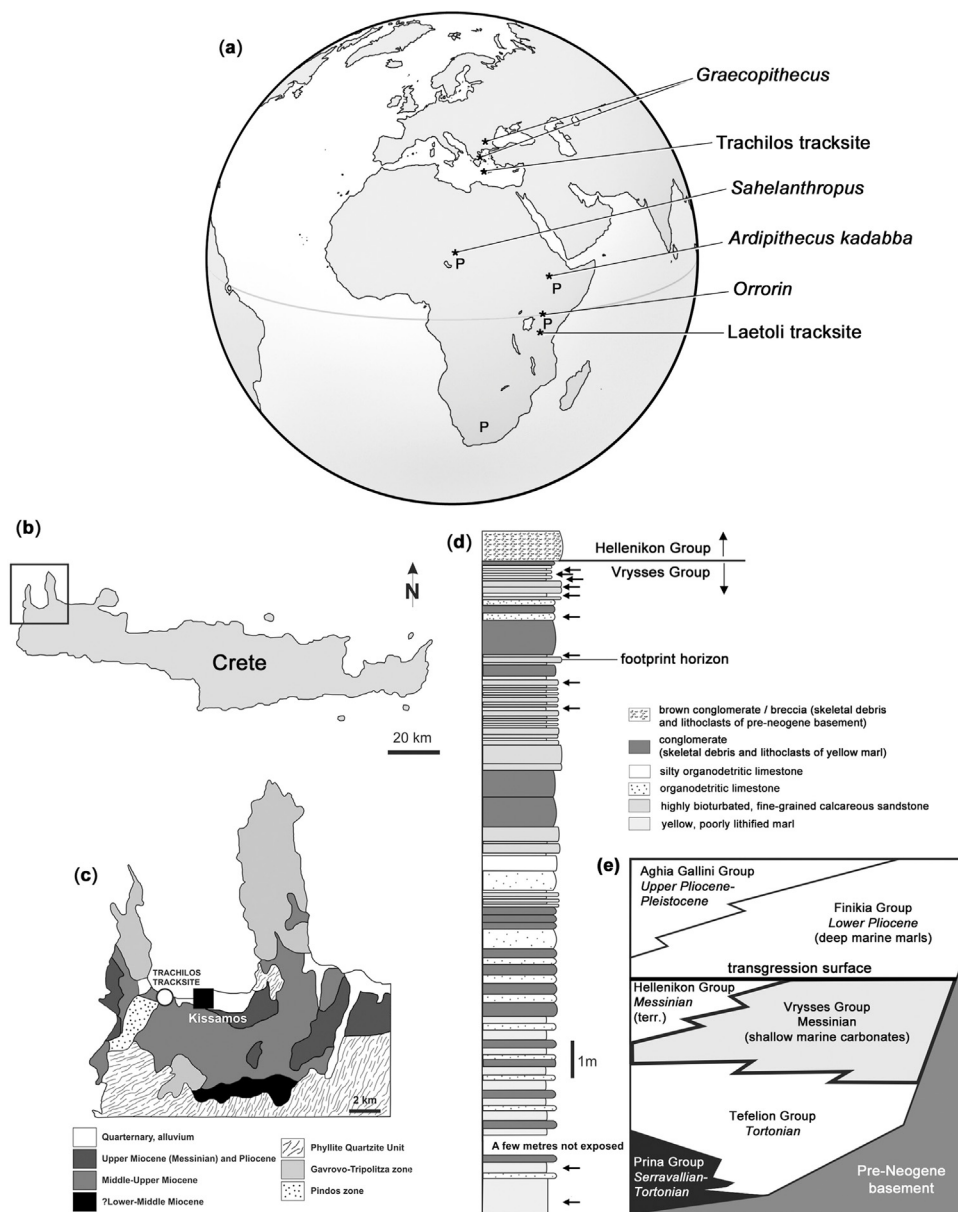


Fig. 1. Location and stratigraphy. (a) Globe showing the locations of the Trachilos and Laetoli tracksites, along with localities of named Miocene taxa interpreted as hominins in the recent literature. The letter P indicates regions (not individual localities) that yield Pliocene hominin fossils. (b) Map of Crete showing region of Trachilos trackway locality in box. (c) Enlargement of area in box showing regional geology (from Freudenthal, 1969; van Hinsbergen and Meulenkamp, 2006) and location of trackway locality. (d) Stratigraphic column through trackway locality, showing levels sampled for foraminifera (small arrows) and the overlying contact with the Hellenikon Group representing the desiccation event of the Messinian Salinity Crisis. (e) Schematic representation of the geology of western Crete, from van Hinsbergen and Meulenkamp (2006).

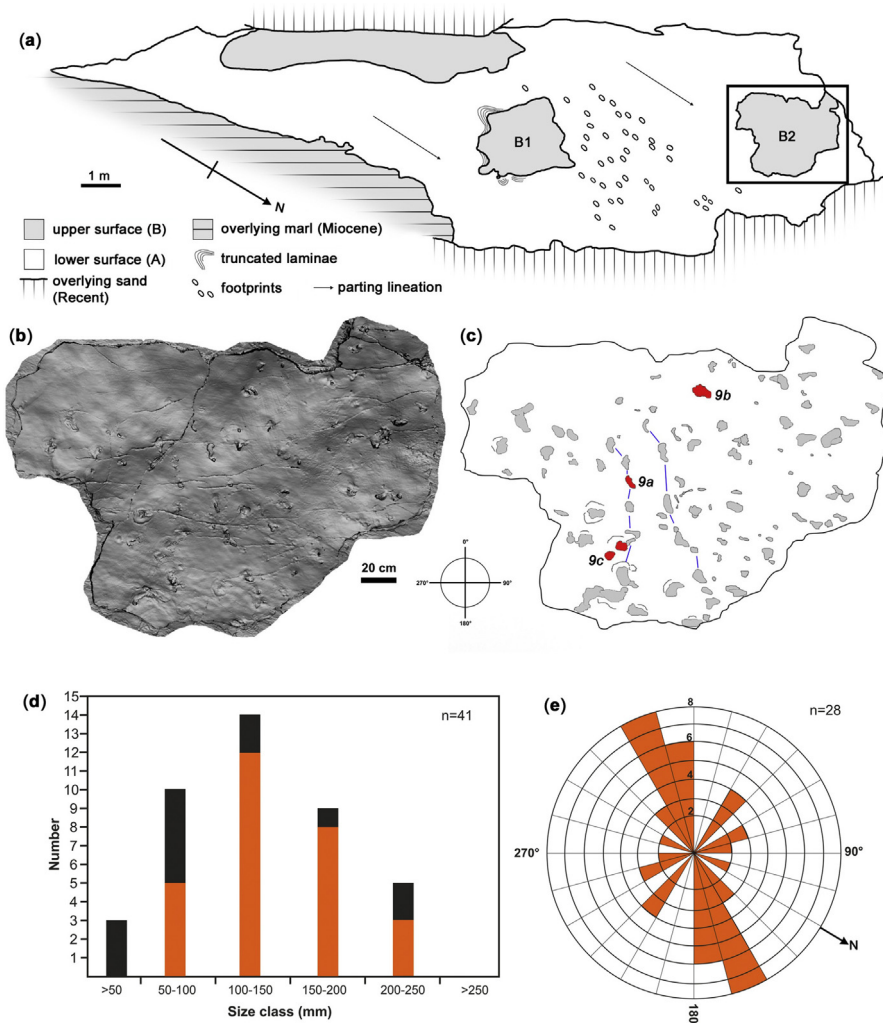


Fig. 2. Site map. (a) Map of track-bearing surface. The grey shaded areas B1 and B2 represent a slightly higher stratigraphic level, but these are erosional remnants produced by a contemporary event, as shown by the truncated laminae round B1. (b) Enlargement of area B2, laser surface scan showing numerous trace fossils as well as undulating surface probably representing large ripples. Wind scour lineation faintly visible in central upper part, running left-right. (c) Schematic drawing of trace fossils on surface. Blue lines indicate two trackways shown in Fig. 7. Red footprints are shown in close-up in Fig. 9. (d) Histogram showing size range (maximum length) of trace fossils. Orange colour indicates trace fossils that can confidently be identified as footprints. (e) Orientation rose showing long axis orientation of those trace fossils that can be confidently identified as footprints.

populations. The comparative populations consist of: (1) 31 3D scans of habitually unshod tracks made by members of the Daasanach people from Ilheret (Kenya; Bennett et al., 2016a); (2) four 3D scans of baboons from Amboseli (Kenya); (3) 11 3D tracks from the G1 trails at Laetoli taken from first generation casts held at the National Museum of Kenya (Bennett et al., 2009); and (4) due to the lack of 3D primate data, 15 mixed species 2D primate images (baboons, gorilla, green monkeys, and chimpanzees) were also included. Although 3D scans were available, only 2D landmarks were extracted using DigTrace, because of the inclusion of 2D primate images in the analysis. The 2D images were first georectified to the orthogonal plane within ArcMap and then landmark data was extracted using tpsDig2 (Rohlf, 2015; <http://life.bio.sunysb.edu/morph/soft-dataacq.html>). Landmark coordinates from all sources were subject to a 2D Generalized Procrustes analysis using PAST (Hammer et al., 2001; <http://folk.uio.no/ohammer/past/>) and subject to a shape-based Principal Components Analysis (Hammer and Harper, 2006). Foraminifera samples were taken from fresh exposures and surfaces above and below track-bearing surfaces; in total 11 samples were analysed for their micropalaeontology. Each sample was about 0.5 kg in weight and

was processed using Glauber's salt. Separated specimens were observed and imaged by SEM.

3. Geological setting and age

The coastal rocks at Trachilos, west of Kissamos Harbour in western Crete (Fig. 1a–c), lie within the Platanos Basin, and present a succession of shallow marine late Miocene carbonates and siliciclastics of the Roka Formation, a local development of the Vrysses Group (Freudenthal, 1969; van Hinsbergen and Meulenkamp, 2006; Figs. 1d, e and 3a, b). At the top, this marine succession terminates abruptly in the coarse-grained terrigenous sedimentary rocks of the Hellenikon Group (Figs. 1d and 3e, f), which formed by the desiccation of the Mediterranean Basin during the Messinian Salinity Crisis (van Hinsbergen and Meulenkamp, 2006), an event dated to approximately 5.6 Ma (Govers, 2009). The succession (Fig. 1d) contains an emergent horizon with well-preserved terrestrial trace fossils and microbially induced sedimentary structures (Fig. 3d) immediately overlying shallow water ripplemark structures (Fig. 3c). Eleven foraminiferal samples were taken at intervals through

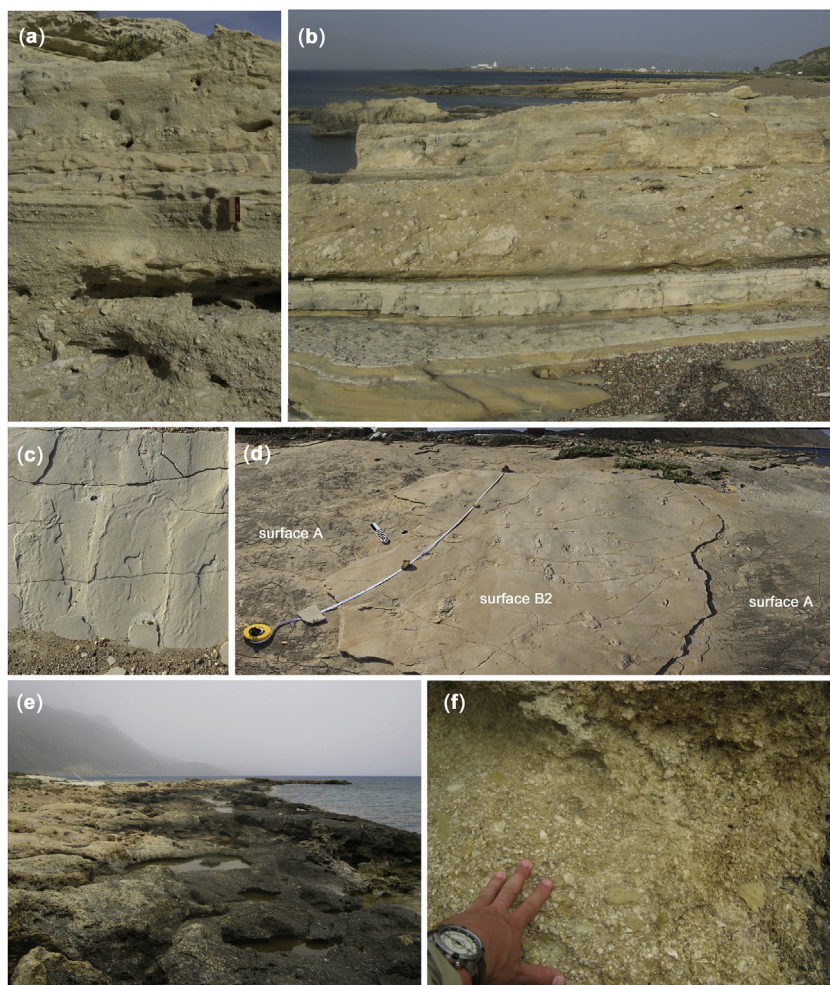


Fig. 3. Deposits from the Trachilos section. (a, b) Lower part of the section, below the trackway horizon. (a) Part of profile with conglomerates, limestones, silty limestones and calcareous sandstones with skeletal elements. (b) Part of profile with thick, unsorted conglomeratic horizon, probably representing a tsunamite. (c) Calcareous sandstone showing ripples with wrinkled crests, indicating very shallow water, about 50 cm below trackway horizon. (d) Footprint surfaces A and B2. (e, f) Calcareous sandstones and conglomerates with breccia-like horizons from the upper part of the section, above the trackway horizon.

approximately 20 m of succession, spanning the tracked horizon and terminating just below the Hellenikon Group conglomerate (Figs. 1d and 4). All these samples yield both *Hastigerina pelagica* and *Globigerina pseudobesa* (Figs. 4 and 5), constraining the samples to a time interval between 8.5 Ma (late Miocene, Tortonian) and 3.5 Ma (early Pliocene, Zanclean; Zachariasse, 1975; Kennett and Srinivasan, 1983; Boudagher-Fadel, 2013). We conclude that the succession at Trachilos can be securely assigned to the Miocene and dated to the time interval 8.5 to 5.6 Ma based on: (1) the end-Miocene Hellenikon Group is the only terrigenous incursion into the marine succession of western Crete during this time interval; (2) the foraminiferan samples lack post-Miocene index taxa; and (3) the Zanclean of Crete is represented by deep-water marlstones not shallow-water carbonates (Freudenthal, 1969; van Hinsbergen and Meulenkamp, 2006). Its position close to the Hellenikon Group contact suggests that it represents the latest part of that interval, immediately prior to the desiccation event (Fig. 4b); to reflect this, we approximate its age as 5.7 Ma. The benthic component of the foraminiferan assemblage contains a large number of keeled representatives of the genus *Elphidium* which indicates a shallow marine environment, no more than 50 m deep with a relatively high salinity (35‰–70‰; Murray, 2006).

The sedimentary succession at the Trachilos tracksite consists of alternating series of conglomeratic beds and intraformational conglomerate/local breccia horizons (with skeletal debris and

lithoclasts); silty limestones; organodetic limestone; fine-grained, highly bioturbated, calcareous sandstones (sometimes with skeletal elements); and yellow, poorly lithified marlstones, together representing a marginal marine environment (Figs. 1 and 3). Horizons with numerous shallow water body fossils (e.g., algae; cf. *Lithothamium*) and trace fossils commonly seen in shallow water environments (e.g., *Thalassinoides* isp.) can be observed in the section. The fossil assemblage also includes bivalves, gastropods, echinoids, ostracods, foraminifera, fish bones and scales, and marine mammal bones.

The emergent horizon forms an exposed surface about 21 m in length and 6 m in maximal width (Fig. 3d), and can also be identified in section in neighbouring outcrops. The immediately underlying strata contain moderately large ripples with microbial mat-related structures (wrinkles) on their crests, suggesting deposition in extremely shallow water (Eriksson et al., 2010; Banerjee et al., 2014). The emergent surface is composed of a lower level (Surface A) carrying two discrete patches of overlying sedimentary rock (Surface B1 and B2), about 2–4 cm thick, with sharply defined edges and upper surfaces that appear to represent a single bedding plane. B1 and B2 are clearly erosional remnants of a once-continuous sediment cover on top of A (Fig. 3d). Surface A reveals parting lineations with a SSW–NNE orientation, and locally shows truncation of fine laminae at the contact with layer B, which suggests that the erosional event that removed most of layer B may

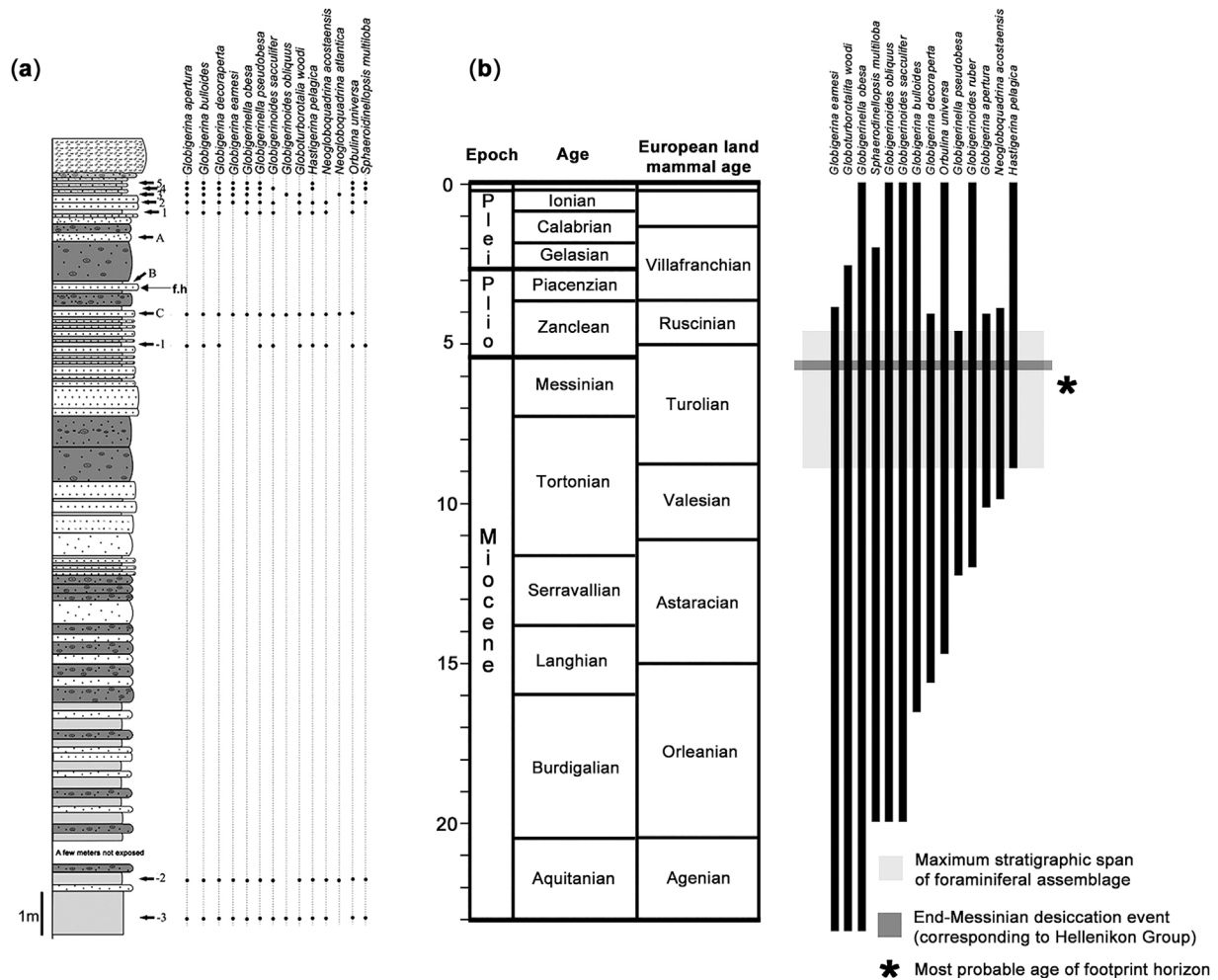


Fig. 4. Foraminiferal assemblage. (a) Diagram of the planktonic foraminifera obtained from different samples above and below the footprint horizon (f, h). Note that all taxa span the footprint horizon. (b) Known stratigraphic ranges of these planktonic foraminifera, arranged in order of first appearance from oldest (left) to youngest (right). The co-occurrence of *Globigerinella pseudobesa* and *Haslerina pelagica* shows that the assemblage cannot be older than late Tortonian or younger than mid Zanclean (pale grey box). Its stratigraphic position immediately below the Hellenikon Group, which represents the end-Messinian desiccation event (dark grey line), suggests that the footprint horizon is late Messinian in age. Numbers on left of time scale indicate age in million years. Plei, Pleistocene; Plio, Pliocene.

have occurred during the period of deposition, not in the recent past when the strata became exposed (Fig. 6). Surfaces A and B dip gently to the east, where A is overlain by a soft, yellow, poorly lithified marlstone. No sedimentary rock overlying B1 or B2 is preserved, but we infer that the marlstone probably covered these patches as well. The hardness contrast between the soft marlstone and the hard, well-lithified surface B2 probably explains the excellent preservation and clean surface of the latter.

In between surfaces B1 and B2 are 42 oval sediment-filled impressions on Surface A, all of approximately similar size and shape, with long axes oriented SSW–NNE (Figs. 2a and 6). The NNE end of many impressions is associated with a small field of ripple crests oriented perpendicular to the SSW–NNE long axis and suggesting NNE flow (Fig. 6). The general configuration of the regional landscape was the same in the Messinian as now, with land to the south and sea to the north; a NNE flow direction, coupled with the complete absence of marine macrofossils in surface A, therefore suggests that this water flow could represent a temporary freshwater flooding event, perhaps a small stream bursting its banks. Some of the impressions are arranged in linear series and we interpret them as poorly preserved tracks. It is uncertain whether they represent under-tracks of primary tracks on now-vanished parts of surface B, or primary tracks made in shallow flowing water prior to the deposition of surface B. Despite

representing the same level, surfaces B1 and B2 have different textures and only B2 preserves ichnofossils (Figs. 2b and 6); this presumably reflects local-scale differences of the substrate. B2 is very hard and has a surface of dense, fine-grained, well lithified calcareous sand, marked by very subtle parallel striations with a SSE–NNW alignment that appear to represent wind scour (Fig. 2b, upper part of slab). Like surface A, surface B contains no marine macrofossils. We interpret surface B2 as representing an area of aerially exposed sand close to the shoreline, possibly part of a small river delta.

4. Tracks

The ichnofossils on surface B2 number more than 50 in total on an area of less than 4 m² (Fig. 2b, c). Their size ranges from less than 50 to more than 200 mm in length (Fig. 2d), but this includes a distinct subset of small and irregular features of uncertain origin. The ichnites that can most readily be identified as footprints range in size from 94 to 223 mm. Although individual trackways are difficult to discern on the densely trampled surface, the majority of footprints show a NE–SW long axis orientation (Fig. 2e). Two identifiable trackways (Fig. 7) conform to this pattern and show that the trackmakers were travelling towards the present-day southwest. Both trackways are narrow and appear to have been

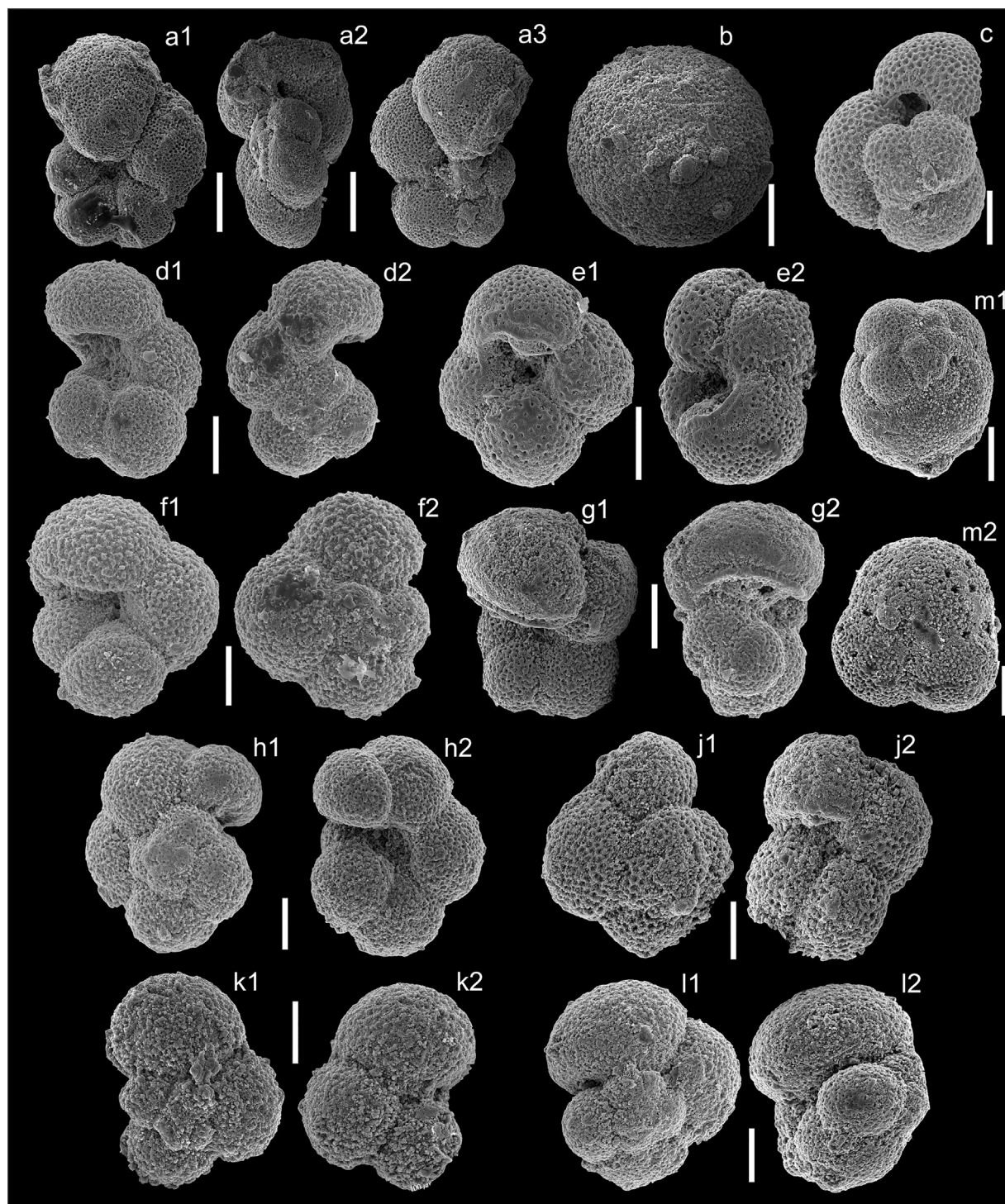


Fig. 5. Foraminifera. Selection of planktonic and benthic foraminifera from different samples. (a1–3) *Hastigerina pelagica* d'Orbigny, sample C; (b) *Orbulina universa* d'Orbigny, sample C; (c) *Globigerinoides sacculifer* (Brady), sample 4; (d1–2) *Globigerinella pseudobesa* (Salvatorini), sample –1; (e1–2) *Globoturborotalita woodi* (Jenkins), sample C; (f1–2) *Globigerina bulloides* d'Orbigny, sample –1; (g1–2) *Neogloboquadrina atlantica* (Berggren), sample C; (h1–2) *Neogloboquadrina acostaensis* (Blow), sample 4; (j1–2) *Globigerina decoraperta* Takayangi and Saito, sample C; (k1–2) *Globigerina eamesi* Blow, sample C; (l1–2) *Globigerinella obesa* (Bolli), sample 4; (m1–2) *Sphaeroidinellopsis multiloba* (Le Roy), sample 4. Scale bars, 100 μm .

formed by a bipedal trackmaker, due to the absence of forelimb tracks. An apparent pair of left and right footprints may have been made by a stationary individual, but we cannot exclude the possibility that this is a chance association (Fig. 8).

The quality of track preservation is variable, but the best specimens have clear displacement rims (expulsion rims) and sharply defined edges (Fig. 9). They are preserved as shallow,

partially excavated, impressions in concave epirelief that also contain pull-up features associated with adhesion of the substrate and ejecta (Figs. 9a, b and 10). They were impressed into a compact and slightly adhesive substrate. Less well-preserved tracks lack detail (Fig. 11) and may have, in some cases, been modified by wave action. The ichnofossils include some large complex structures, possibly representing multiple overprints.

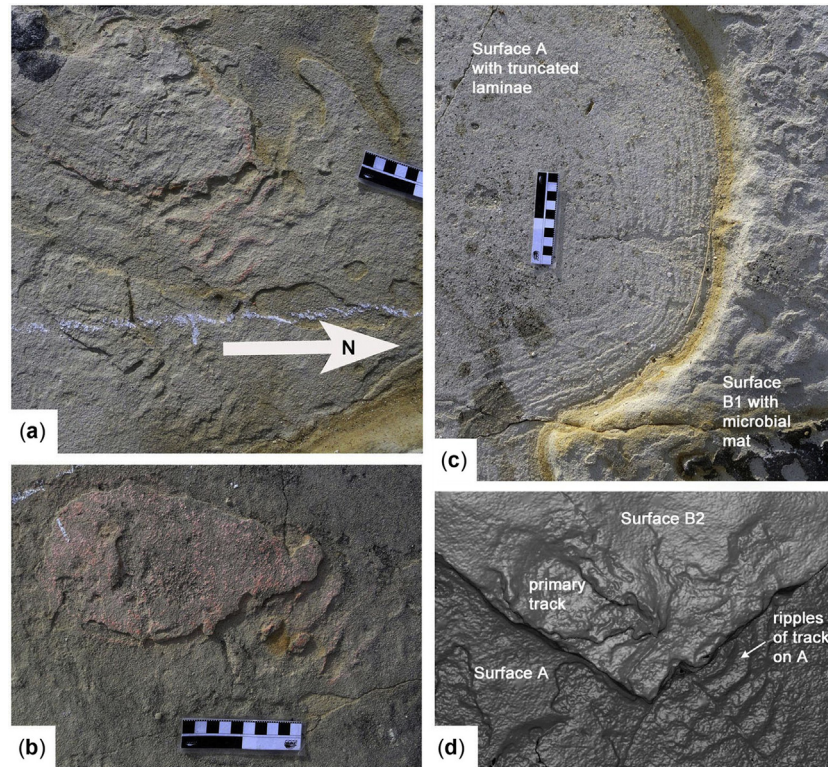


Fig. 6. Surface A. (a, b) Individual footprints from surface A showing lack of anatomical detail and association with ripple patches. (c) Truncated laminae at the contact between surfaces A and B1. (d) Association between a footprint on Surface B2 and a ripple patch on surface A. This could indicate that the footprints on A are underprints, though the association may also be fortuitous.

The tracks are similar in size and have consistent outlines across all the specimens. This is an oblique subtriangular shape formed by the combination of a heart-shaped, plantigrade sole with a narrow, tapering heel region, and an asymmetrical digit region with a large hallux and progressively smaller lateral digits that are all attached to the anterior margin of the sole. The tracks are therefore strongly

entaxonic (Fig. 9). There is no significant divide between the impressions of the first digit and lateral digits, although in well-preserved prints a gap of a few millimetres is sometimes visible (Fig. 9c), but in other examples the impressions are confluent (Fig. 9a, b). Both the entaxy and the lack of a gap between the hallux and other digits are evident even in the poorly preserved

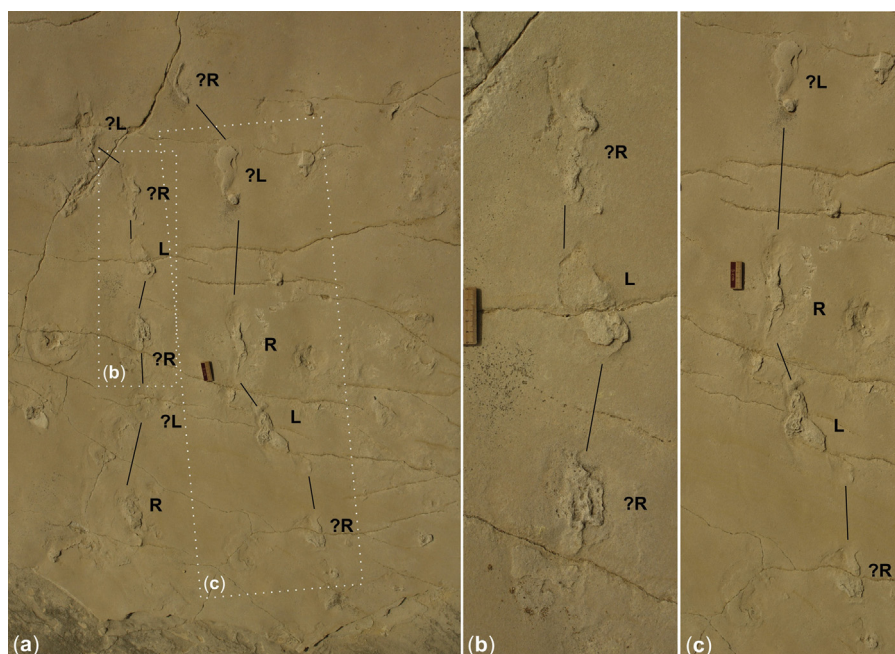


Fig. 7. Trackways. (a) Two trackways from surface B2, details shown in (b) and (c). R and L indicate right and left footprints.



Fig. 8. Photograph of two prints possibly representing a static stance of one individual.

prints (Fig. 11). None of the prints shows claw impressions. In a few prints the heel impression appears bulbous rather than narrow (Fig. 9a, c), but this is an effect produced by an unusually large expulsion rim; when the expulsion rim is small, the narrow and pointed shape of the heel impression is clearly visible (Fig. 9b). Three especially well-preserved prints (Fig. 9a–c) provide morphological information about the feet of the trackmaker. The print in Fig. 9a is the smallest, with a length of approximately 105 mm. It has a strongly developed expulsion rim around the heel impression, with a flat infill across most of the sole and two large blobs of adhering sediment in the heel region and behind the ball. The track shows a well-preserved set of digit impressions as well as part of a ball impression. The digit impressions form a strongly asymmetrical, curving array. The first digit impression is morphologically distinctive, larger than the other impressions, and slightly offset from them. There appear to be four lateral digits, though the boundaries between their impressions are somewhat indistinct. It is noteworthy that even though the tips of the digits have dug into the sediment, there is no trace of claw impressions. The track shown in Fig. 9b is a larger print, approximately 135 mm long. Much of the plantar surface appears to be preserved, apart from an L-shaped patch of adhering sediment with a long limb extending along the mid-lateral part of the sole, and a short limb marking the crease between sole and digits. The plantar surface includes a deep, rounded ball impression with its own small expulsion rim. The first digit impression is deep; it has a clear outline showing a narrow neck and an expanded, asymmetrically trapezoidal to oval pad. The impressions of digits II–IV have well-defined distal ends, but become less clear proximally. Digits II and III are slender and parallel-sided with squared-off ends; the impression of digit IV is shorter and oval with a slightly pointed tip. There is no clear impression of digit V. The depth of the ball impression and the apparent deflection towards the right of the digit impressions suggest that the foot rotated clockwise on the ball during the step. Fig. 9c is one of the largest prints, approximately 154 mm long. It divides into separate anterior and posterior parts, but the presence of circular displacement features surrounding the entire print show that both part were generated by a single footfall. The anterior part includes impressions of a hallux and four lateral digits.

4.1. Comparative analysis

The Trachilos tracks appear to have been made by a bipedal trackmaker with plantigrade, entaxonic, five-toed feet that did not leave claw impressions. The first digit of the foot was bulbous whereas digits II–V were slender, with no significant gap between the hallux and digit II. A well-developed ball was present. Certain

potential interpretations can be ruled out because of gross morphological differences: these include artiodactyls, perissodactyls, and digitigrade carnivores such as cats and dogs. However, some plantigrade pentadactyl mammals could in principle produce tracks similar to those from Trachilos. The main alternatives that need to be considered, given the Neogene Old World context of the tracks, are monkeys, apes and bears (Fig. 12).

Bears and certain other Carnivora have pentadactyl hind feet with heart-shaped soles and short toes, somewhat similar to the print morphology described here, and their claws do not always leave impressions. However, carnivore prints are rarely entaxonic, and certainly never to the degree exhibited by the Trachilos prints; the carnivore hallux is not morphologically distinctive and is at most marginally bigger than adjacent digits (Fig. 12a, b). The hind feet of non-hominin primates have strongly divergent thumb-like halluces, always set back from the relatively long lateral digits. Chimpanzees (Fig. 12e) produce characteristic L-shaped footprints with a wide gap between the hallux and curled lateral digits (Harcourt-Smith and Aiello, 2004; Berge et al., 2006; Meldrum et al., 2011). In the footprints of Old World monkeys such as vervets the hallux is usually abducted (Fig. 12c), but even when it is adducted its proximal position along the side of the sole is obvious. The same applies to gorilla footprints (Sénut, 2010), even though these are more hominin-like in proportions with shorter toes and a smaller gap between hallux and digit 2 (Fig. 12e). Non-hominin primate prints typically lack a ball impression.

The Trachilos tracks are bipedal and thus appear to discount both carnivores and non-hominin primates due to their habitual quadrupedalism. The endemic Miocene hominoid *Oreopithecus* from the Vallesian – early Turolian of the Tuscany-Sardinia archipelago, which has sometimes been interpreted as bipedal, is a relatively near neighbour of the Trachilos tracks in time and space, and should thus be evaluated as a potential track maker. However, because it has an extremely divergent hallux that could not be fully adducted (Köhler and Moyà-Solà, 1997; Russo and Shapiro, 2013), it is unlikely that *Oreopithecus* could have produced footprints like those at Trachilos.

The Trachilos tracks resemble hominin prints (Leakey and Hay, 1979; Harcourt-Smith and Aiello, 2004; Bennett et al., 2009, 2016a, b; Lockley et al., 2016) due to their plantigrade and entaxonic nature. By contrast, the morphology of the sole print is not especially hominin-like: compared to a modern human sole print it is proportionately shorter, with a narrow tapering heel, and lacks a permanent arch. The prints are also smaller than any known hominin print population. To explore the morphology of the tracks, they were compared using a landmark-based approach with both non-hominin primate and hominin tracks. Fig. 13a shows the landmark distribution; the key differences between the non-hominin primate populations and all others lie in the inter-landmark distances L1–L2 and in the length of the tracks L1–L4 (Fig. 13b). There is also considerable variance in the placement of L3 (degree of hallux abduction) and consequently in the placement of L9. This is reflected in the Principal Components Analysis, with 77.4% of the variance explained by the first and second components. This corresponds to the variation in the placement of landmarks L2 and L3. There is clear separation between the non-hominin primate and hominin populations with the Trachilos tracks plotting with the hominin ones primarily due to the distal placement of landmark L2 and the adducted L3 (hallux) divergence. It is also worth noting the greater similarity in heel shape between the Trachilos tracks and the hominin controls. These results are robust across different landmark placement associated with different users and with the inclusion and exclusion of the 2D primate tracks. The implication is that there are greater anatomical similarities between the Trachilos tracks and those of hominins than there are with the non-hominin primate control group.

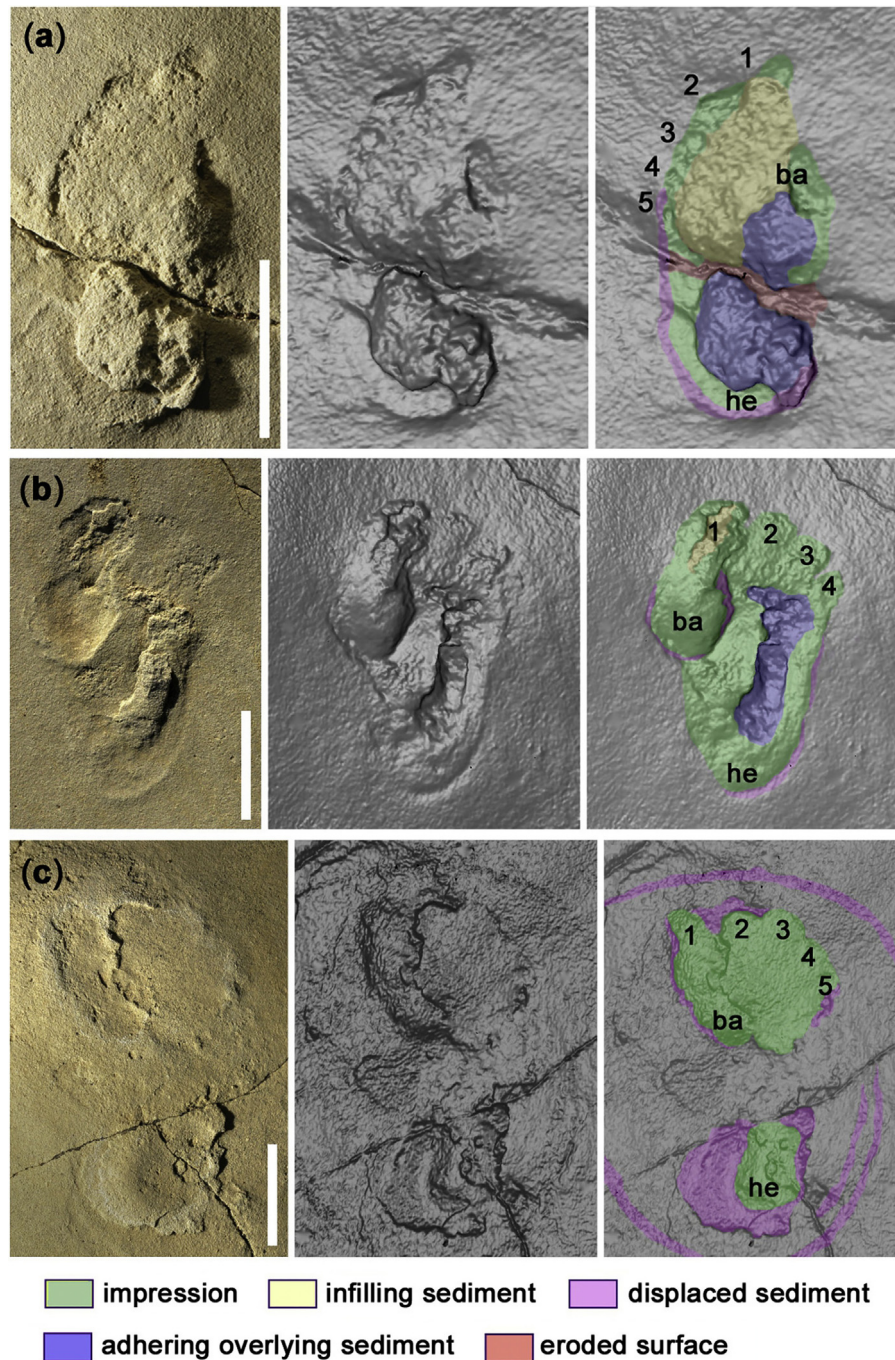


Fig. 9. Well-preserved footprints. (a–c) The three most well-preserved footprints from surface B2, each shown as a photo (left), laser surface scan (middle) and scan with interpretation (right). a was made by a left foot, b and c by right feet. Scale bars, 5 cm. 1–5 denote digit number; ba, ball imprint; he, heel imprint.

5. Interpretation and implications

The characteristics of the *Trachilos* footprints that need to be explained are: bipedality and plantigrade posture; pentadactyly with entaxy and an absence of claws; the distally attached and non-divergent bulbous first digit and short lateral toes; and the presence of a distinct ball in some of the tracks. The morphometric analysis suggests a closer affinity to hominin track outlines than to those of extant non-hominin primates. This leaves us with two possible interpretations:

1. The *Trachilos* tracks may have been made by a phylogenetically basal member of the clade Hominini. This interpretation

explains the combination of unique hominin characteristics in the anterior part of the foot (pronounced entaxy, non-divergence and distal position of the hallux, the shape of the hallux and its size relationship to the ball, as well as the shapes of the distal ends of digits 2–4) with a rather generic sole that is relatively short, lacks an arch and has a narrow, tapered heel. Under this interpretation the tracks would represent a small, primitive, habitually bipedal hominin with hominin-like pedal digits and ball combined with an ape-like sole lacking a bulbous heel. Interestingly, the non-divergent hallux and short lateral digits of the *Trachilos* tracks are absent in the foot skeleton of *Ardipithecus ramidus* known from Ethiopia (Lovejoy et al., 2009a, b), which is more than a million years younger (White et al.,

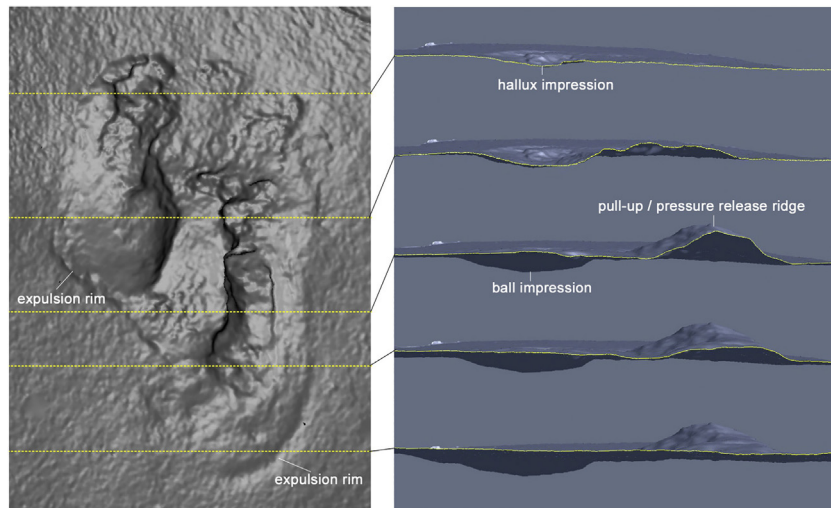


Fig. 10. Three-dimensional structure of a print. Left, laser scan of one of the best preserved footprints (see also Figs. 9 b and 12 g). Right, transverse sections showing concave and convex structures.

2009). The age of the Trachilos footprints, though strikingly early, is not problematic for this hypothesis: assuming an age of slightly more than 5.6 Ma (Fig. 14), they are approximately coeval with *Orrorin* and somewhat younger than *Sahelanthropus* (Sénut et al., 2001; Brunet et al., 2002; Almécija et al., 2013). Virtually nothing is known about the foot morphology of the Miocene African hominins and no hominin trackways of this age are yet known from Africa. Until very recently the evidence for hominins in the Miocene European body fossil record was at best ambiguous (Spassov et al. 2012), but while this paper was in review the early Messinian primate *Graecopithecus*, represented by two fragmentary specimens from savannah

environments in Greece and Bulgaria (Böhme et al., 2017), was reinterpreted as a probable hominin based on dental characteristics (Fuss et al., 2017). With dates of 7.175 Ma for the Greek mandible and 7.24 Ma for the isolated Bulgarian tooth (Böhme et al., 2017), *Graecopithecus* is probably rather older than the Trachilos footprints. It is obviously highly relevant to the interpretation of the prints (Fig. 1a), but the fragmentary nature of the specimens and the absence of postcranial material limit the conclusions that can be drawn from it at present.

2. Alternatively, we could look towards a hitherto unrecognized primate, potentially unrelated to the Hominini, but possessing overall morphological similarities with this tribe. The hominin-

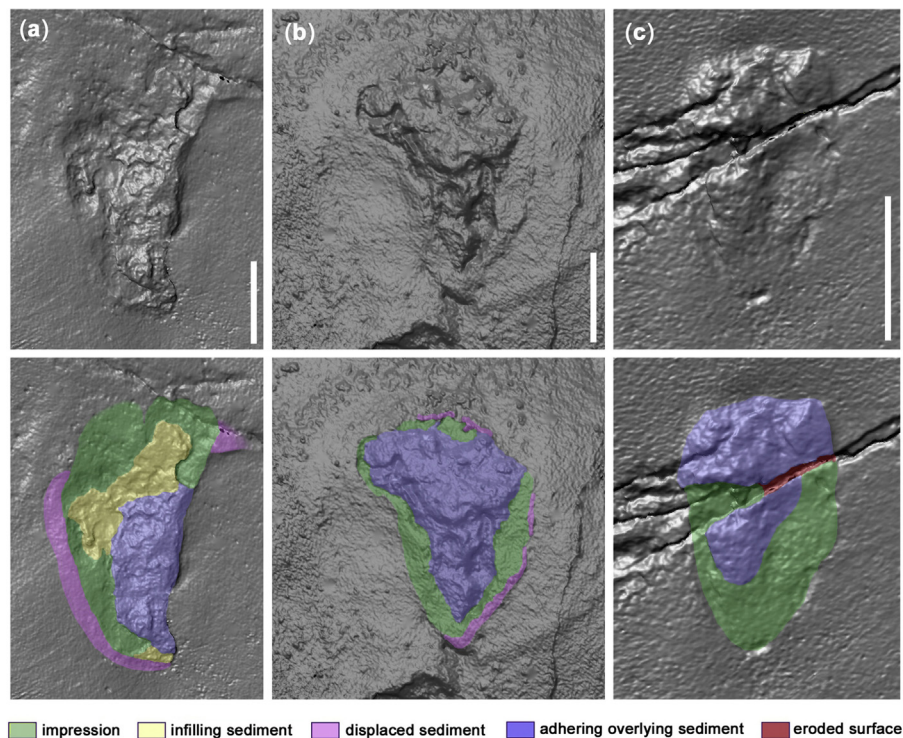


Fig. 11. Less well-preserved prints. Three footprints from Surface B2 showing lack of anatomical detail, but same general shape as the prints in Fig. 9. a and c were made by left feet, b by a right foot. Scale bars, 5 cm.

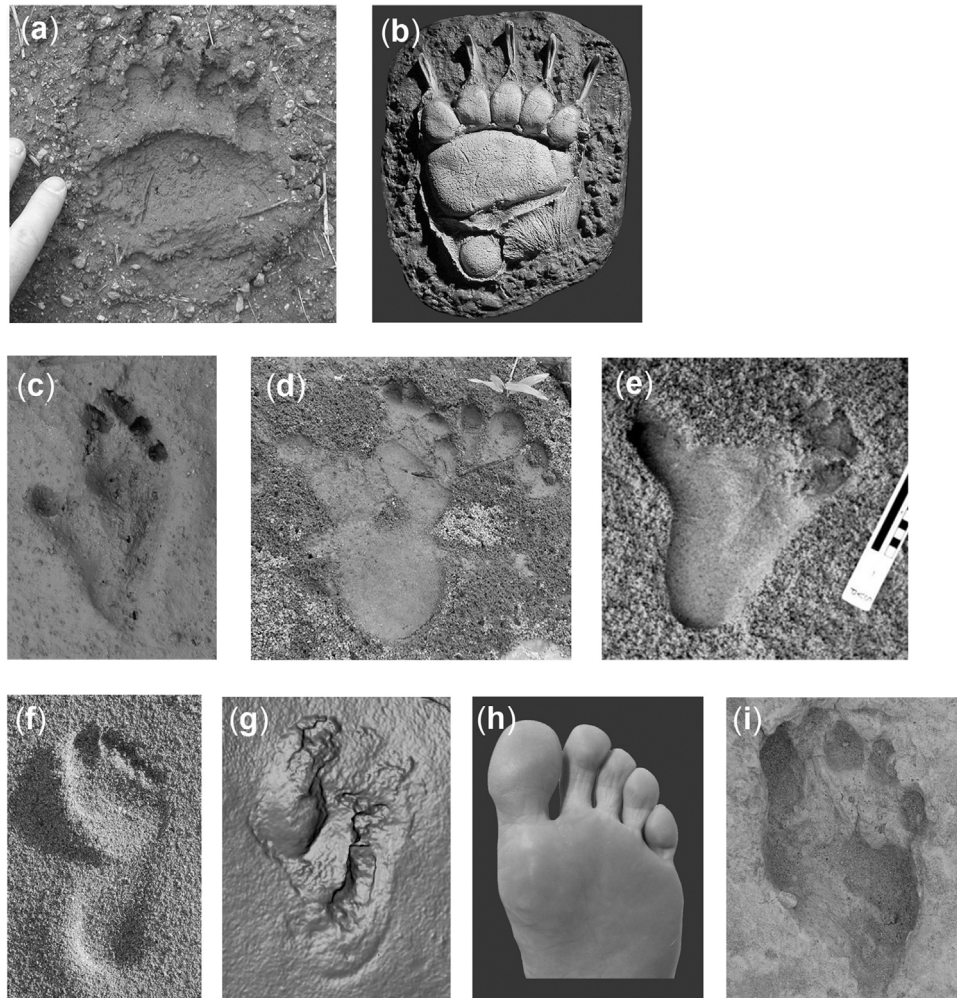


Fig. 12. Comparison with different trackmakers. Comparison of *Trachilos* footprint with bears (top), non-hominin primates (middle), and hominins (bottom). (a) Brown bear manus print, photo by A.A. (b) Cast of grizzly bear manus print, photo by M.L. In bears (and other Carnivora) the hallux is morphologically similar to digit 2. (c) Vervet monkey pes print, photo by G.G. (d) Lowland gorilla pes and knuckle prints, photo by Julie Dewilde. (e) chimpanzee pes print, from Meldrum et al. (2011). In non-hominin primates the hallux is morphologically distinctive but separated from the other digits by a wide gap. (f) modern human pes print, photo by G.N. (g) *Trachilos* footprint shown in Fig. 9b. (h) modern human foot, photo by P.E.A. (i) Archaic *Homo* footprint from Ileret, from Bennett et al. (2009). In hominins, the hallux is large and morphologically distinctive but positioned close to digit 2; there is also a distinct ball.

like characteristics, particularly the anterior placement of the first digit, would reflect an example of convergent evolution, a familiar phenomenon in the fossil record (Emery and Clayton, 2004; Lockley et al., 2008; Parker et al., 2013). Fossil apes are not uncommon in the Miocene of Europe and there is a considerable diversity of forms, ranging biostratigraphically from the early middle Miocene to the late Miocene (middle Turolian; Harrison, 2010; Sénut, 2010; Spassov et al., 2012; Böhme et al., 2017). The subsequent disappearance of apes from the region has been attributed to climatic drying and cooling. Interestingly, apes persist somewhat longer in Eastern than in Western and Central Europe. It has been argued that these late eastern forms are adapted to drier and more open landscapes (Casanovas-Vilar et al., 2011; Spassov et al., 2012). The large-sized genus *Ouranopithecus*, present in Greece and adjacent regions during the late Miocene (9.6–8.7 My; Koufos and de Bonis, 2005), has been proposed as a close relative of the Hominini or Hominidae (hominins, chimpanzees and gorillas), though this is debated (de Bonis and Koufos, 1993; Begun et al., 2012; Koufos, 2015). However, its pedal morphology and locomotory behaviour are unknown, as most of the available fossils pertain to craniodental material. This alternative hypothesis is thus not implausible, but

it should be noted that it is not positively supported by data from the pedal skeleton of any known European primate.

The first of these interpretations is clearly more straightforward. There is nothing about the character complement or morphometrics of the *Trachilos* prints that positively suggest convergence with hominin morphology and, as noted above, there is no positive body fossil evidence for the existence of such a convergently hominin-like primate. In a formal sense interpretation 2 thus fails the Occam's Razor test of explanatory parsimony. However, we feel it should nevertheless be entertained, because nature is not always parsimonious and, more importantly, interpretation 1 carries major biogeographical implications that also need to be examined critically.

During the late Miocene, Crete was separating from the mainland by extension faulting creating the Aegean Sea basin (van Hinsbergen and Meulenkamp, 2006). Late Miocene (Valesian-Turolian) faunas from Crete contain large non-endemic mammals such as hyaenids, proboscideans (gomphotheres and deinotheres), a hipparionine horse, pigs, a cervid, a bovid and tragulids (Benda et al., 1970; de Bruijn et al., 1971; Kuss, 1976; Leinders and Meulenkamp, 1978; van der Made, 1996; Athanassiou, 2004;

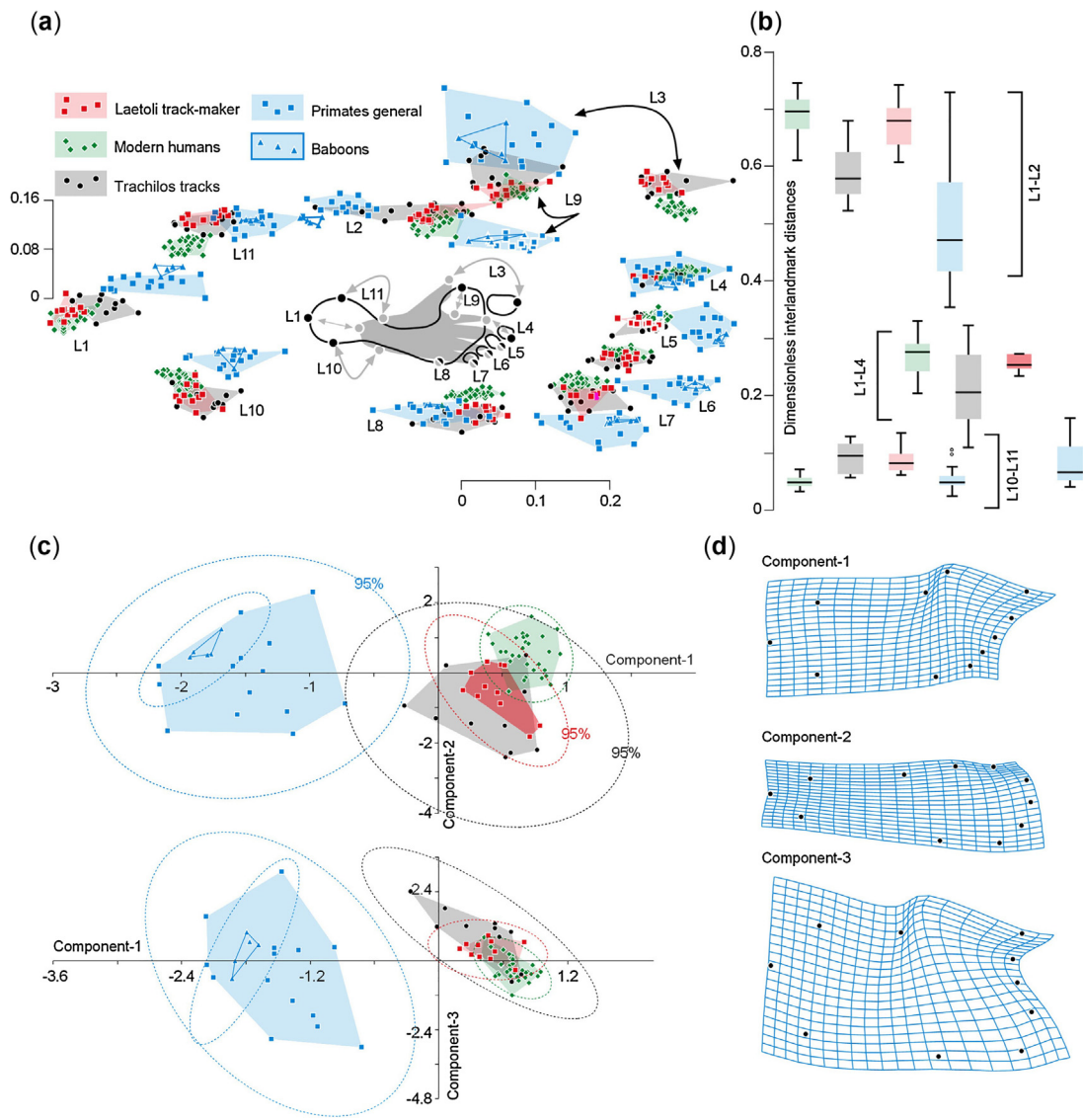


Fig. 13. Morphometric analysis. (a) Distribution of 11 landmarks for the various control samples and the Trachilos tracks (N = 10). (b) Key inter-landmark distance post-Procrustes transformation. (c, d) Principal components analysis and principal warps.

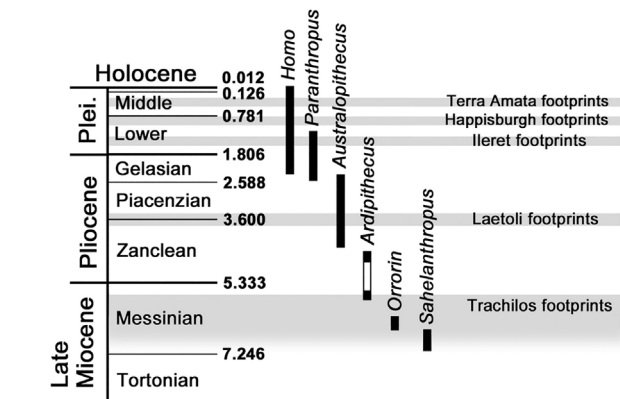


Fig. 14. Trackway time scale. Time scale showing age of Trachilos trackway locality and some important hominin trackway localities, superimposed on time ranges for major fossil hominin taxa. Note that the lower age boundary for Trachilos is poorly defined, but that the true age of the locality probably is close to 5.7 my. See also Fig. 4.

Poulakakis et al., 2005a; Iliopoulos et al., 2012), suggesting that a land bridge still existed. Molecular biogeographic studies of extant lizards and gastropods suggest final separation between western Crete and mainland Greece by 5 million years BP (Poulakakis et al., 2005b). The Trachilos trackmaker may thus have inhabited a south-east-trending peninsula of the Greek mainland rather than an island. But whatever the exact timing of the separation process, it is clear that Crete never had a direct connection to the southern shore of the Mediterranean; its late Miocene mammal fauna, including the Trachilos trackmaker, must have arrived from the north. Identification of the prints as hominin thus implies a minimum range extension for this group from Africa to encompass the Levant, Asia Minor and southern Balkans (Fig. 1a).

The question is whether such a range extension is credible. From a present-day perspective it seems doubtful, because the known Miocene hominin localities in Chad, Ethiopia and Kenya are separated from the north-east Mediterranean coast by the expanse of the Sahara Desert, with only the Nile valley and Levant providing a tenuous (and discontinuous) chain of mesic environments between the two. However, conditions in the Messinian were very different, with monsoonal rainfall over north-east Africa creating

well-watered environments that drained northwards through the Eonile and Eosahabi (in Libya) rivers, and south into Lake Chad, which was much larger than today (Griffin, 2001). There is no evidence for inhospitable environments that would have created a dispersal barrier to early hominins. We conclude that a hominin interpretation of the Trachilos footprints is not biogeographically implausible.

6. Conclusion

We have presented two alternative interpretations of the ichnites found at Trachilos. The hypothesis that the Trachilos trackmaker was a basal hominin carries substantial implications for early hominin biogeography, as well as for the development of bipedality and the entaxonic foot (Lockley et al., 2016). Given the challenging nature of this potential interpretation it might be considered prudent to delay taxonomic assignment. However, despite the fact that the full 3D anatomy of these tracks is not optimally preserved, they are not poor trace fossils. Their outlines are particularly clear and form the basis of the morphometric analysis presented here. Better and more numerous trace fossils are always to be desired, but equally one cannot ignore the currently available evidence and their potential implications, however challenging they may be. Further prospecting for ichnofossils and body fossils in the late Miocene of the eastern Mediterranean area has potential to resolve the identity of the Trachilos trackmaker and should be an urgent priority.

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